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1 **Title**

2 Potential lethal and non-lethal effects of predators on dispersal of spider mites

3

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Abstract Predators can affect prey dispersal lethally by direct consumption or non-lethally by making prey hesitate to disperse. These lethal and non-lethal effects are detectable only in systems where prey can disperse between multiple patches. However, most studies have drawn their conclusions concerning the ability of predatory mites to suppress spider mites from observations of their interactions on a single patch or on heavily infested host plants where spider mites could hardly disperse toward intact patches. In these systems, specialist predatory mites that penetrate protective webs produced by spider mites quickly suppress the spider mites, whereas generalist predators that cannot penetrate the webs were ineffective. By using a connected patch system, we revealed that a generalist ant, *Pristomyrmex punctatus* Mayr (Hymenoptera: Formicidae), effectively prevented dispersal of spider mites, *Tetranychus kanzawai* Kishida (Acari: Tetranychidae), by directly consuming dispersing individuals. We also revealed that a generalist predatory mite, *Euseius sojaensis* Ehara (Acari: Phytoseiidae), prevented between-patch dispersal of *T. kanzawai* by making them hesitate to disperse. In contrast, a specialist predatory mite, *Neoseiulus womersleyi* Schicha, allowed spider mites to escape an initial patch, increasing the number of colonized patches within the system. Our results suggest that ants and generalist predatory mites can effectively suppress *Tetranychus* species under some conditions, and should receive more attention as agents for conservation biological control in agroecosystems.

Keywords Dispersal • Anti-predator behavior • Conservation biological control • Density-mediated effects • Trait-mediated effects • *Tetranychus kanzawai*

30 Introduction

31

32 Although successful dispersal is crucial for prey organisms that utilize patchy resources, predators
33 prevent prey dispersal by consuming dispersing individuals (Young and Lockley 1988; Bonnet et al.
34 1999; Hiddink et al. 2002) or making them hesitate to disperse. Prey individuals that stay in a refuge
35 suffer reduced feeding time (Koivula et al. 1995; Dill and Fraser 1997), reduced mating opportunities
36 (Sih 1994; Cooper 1999), and physiological costs from unfavorable conditions in refuges (Wolf and
37 Kramer 1987; Martin and Lopez 1999). Such non-lethal effects (trait-mediated effects) of predators
38 can sometimes be comparable to those of direct consumption (density-mediated effects) (Lima 1998;
39 Werner and Peacor 2003; Nelson et al. 2004; Preisser et al. 2005; Creel and Christianson 2008).

40 Spider mites in the genus *Tetranychus* are major agricultural pests (Jeppson et al. 1975;
41 Helle and Sabelis 1985; Johnson and Lyon 1988) that live in three-dimensional protective webs on
42 leaf surfaces (Saito 1983). In response to deteriorating leaves, mated females disperse, mainly by
43 walking to a new resource (Brandenburg and Kennedy 1982; Kennedy and Smitley 1985; Margolies
44 and Kennedy 1985), although they disperse aerially under some conditions (Margolies and Kennedy
45 1985; Smitley and Kennedy 1985). Because a single foundress can establish a new colony, dispersal
46 of mites can critically affect population structure in agroecosystems. Predatory mites are promising
47 biological control agents against spider mites in both conservation and augmentative biological con-
48 trol strategies (e.g. McMurtry 1982, 1992); therefore, understanding their effects on the dispersal of

49 spider mites is crucially important.

50 Nevertheless, most previous conclusions concerning the ability of predatory mites to sup-
51 press spider mites seem to have been drawn from observations of their interactions on a single patch
52 or on heavily infested host plants, i.e. systems where spider mites could hardly disperse toward intact
53 patches. In these systems, specialist predatory mites that can penetrate spider mite webs (Sabelis and
54 Bakker 1992) can easily suppress the spider mites (e.g. Chant 1961; Hamamura 1986), leading such
55 studies to suggest that specialist predatory mites are effective biological control agents. In contrast,
56 generalist predatory mites that are hindered by the protective webs of spider mites (Osakabe 1988;
57 McMurtry and Croft 1997; Ozawa and Yano 2009) seem ineffective for suppressing spider mites, and
58 thus their effects on spider mite dispersal remains unexplored. We question these well-accepted con-
59 cepts for two reasons. First, generalist predatory mites readily prey on spider mites outside their
60 webs (Yano 2012; Otsuki and Yano 2014) and therefore may interrupt spider mite dispersal by con-
61 suming dispersing mites or by making spider mites hesitate to disperse. Second, because specialist
62 predatory mites induce dispersal of spider mites (Bernstein 1984; Grostal and Dicke 1999; Oku et al.
63 2004; Bowler et al. 2013), specialist predators may increase the spread of spider mite colonies. These
64 putative density- and trait-mediated effects of predators on spider mites are detectable only in sys-
65 tems where dispersal of mites toward intact patches is allowed.

66 We used four species in this study: the spider mite *Tetranychus kanzawai* Kishida (Acari:
67 Tetranychidae), the specialist predatory mite *Neoseiulus womersleyi* Schicha (Acari: Phytoseiidae),

68 the generalist predatory mite *Euseius sojaensis* Ehara, and the generalist ant *Pristomyrmex punctatus*
69 Mayr (Hymenoptera: Formicidae). *Neoseiulus womersleyi* and *E. sojaensis* are native predators of *T.*
70 *kanzawai* in Japan (Hamamura 1986; Osakabe et al. 1986; Amano 1996). *Pristomyrmex punctatus* is
71 a potential predator of *T. kanzawai* (Otsuki and Yano 2014) which often co-occurs with *T. kanzawai*
72 on wild plants such as *Cayratia japonica* (Thunb.) Gagnep (Vitaceae) (Yano, personal observation).
73 All of these species are ambulatory dispersers, so we can easily observe their interactions in micro-
74 cosms of connected patches. Using this system, we examined the following two hypotheses: (i) gen-
75 eralist ants and predatory mites that cannot penetrate spider mite webs can nonetheless prevent dis-
76 persal of *T. kanzawai*, and (ii) specialist predatory mites that penetrate spider mite webs may promote
77 dispersal and patch colonization by *T. kanzawai* in the system.

78

79 **Materials and methods**

80

81 **Animals**

82

83 We collected individuals of *T. kanzawai* from convolvulus *Calystegia japonica* Choisy (Convolvu-
84 laceae) in Kyoto, Japan. The population was then maintained on expanded primary leaves of kidney
85 bean, *Phaseolus vulgaris* L. (Fabaceae), which were pressed onto water-saturated cotton in Petri
86 dishes (90 mm in diameter, 14 mm in depth; hereafter “leaf discs”) to prevent mites from escaping.

87 We collected *N. womersleyi* from *Rosa centifolia* L. (Rosaceae) in Nara, Japan. The population was
88 reared on leaf discs that were infested with *T. urticae* as prey (30–50 female adults and individuals of
89 other stages per leaf). We collected *E. sojaensis* from kudzu vines, *Pueraria lobata* (Willd) Ohwi, in
90 Kyoto and reared them on tea pollen on leaf discs. The leaf discs were placed in transparent plastic
91 containers.

92 We collected 10,000 to 20,000 *P. punctatus* ants from a decayed tree on Mt. Yoshida in
93 Kyoto and divided them into colonies of ca. 500 ants each. Since *P. punctatus* does not have a queen,
94 and the workers can reproduce thelytokously (Mizutani 1980; Itow et al. 1984), we can consider ant
95 individuals collected from one colony as an inbred strain that has minimal genetic variation, and we
96 can easily replicate ant colonies with a fixed number of workers in individual microcosms. Each
97 colony was reared in a microcosm constructed from a transparent plastic container (220 × 300 × 60
98 mm; Fig. 1). We coated the interior walls of the container with talc powder to prevent ants from es-
99 caping. A Petri dish (85 mm in diameter, 11 mm in depth) with a 6-mm plaster layer on the bottom
100 was used as an artificial ant nest. The dish cover was painted with red pigment to encourage settle-
101 ment. We added water on the plaster twice a week to maintain moisture. The ants were fed water and
102 honey ad libitum and freshly killed mealworms every week as a protein source to promote worker
103 reproduction.

104 All mites and ants were reared at a constant temperature of 25°C, with 50% relative humid-
105 ity, and a L16:D8 photoperiod. All experiments were conducted under these conditions.

106

107 Do ants prevent dispersal of spider mites?

108

109 To examine whether the generalist ant *P. punctatus* prevents dispersal of spider mites, we replicated
110 ant microcosms using two-patch setups (Fig. 1). We introduced 10 mated, 2-day-old female members
111 of *T. kanzawai* (hereafter “*T. kanzawai* females”) onto each of 33 bean leaf squares (20×20 mm;
112 initial patches), and allowed them to build webs. Since preliminary tests showed that *T. kanzawai*
113 females in the absence of ants start dispersing from the setup 24 h after the introduction, and that
114 webs build by 10 females for 24 h are effective against ant predation (also see Otsuki and Yano 2014),
115 we connected each leaf to another leaf square (30×30 mm; second patches) with a Parafilm bridge
116 (20×30 mm; Fig. 1) after 24 h of the introduction. By connecting patches with a non-food flat sub-
117 strate on which spider mites cannot construct protective webs, we simulated mite dispersal from an
118 infested patch to an intact patch via a hostile environment without webs. The second patch was larger
119 than the initial one because a preliminary test showed that the larger patch size was necessary to re-
120 tain dispersed females on second patches during the experimental period. Each setup was placed on
121 wet cotton in a square dish ($87 \times 125 \times 8$ mm). Because of the surrounding water barrier, *T.*
122 *kanzawai* females could disperse only by walking across the bridges.

123 For the ant treatment ($n = 17$), we placed each dish in the microcosm 50 mm away from an ar-
124 tificial ant nest (Fig. 1). For the non-ant treatments ($n = 16$), we placed each dish in the microcosm

125 with an empty artificial ant nest, talc powder, and water to control for possible environmental biases.
126 Ants could easily access the spider mite leaves by walking across the wet cotton in the dish. About
127 10% of the ants were active and out of the nest in each colony (Otsuki, personal observation). To
128 eliminate the possible effect of learning, we used each colony only once.

129 After 3 days, when the differences between treatments were most conspicuous after the place-
130 ment in microcosms, we recorded the number of surviving *T. kanzawai* females on each patch and on
131 the bridge. We calculated the proportion of surviving females in the microcosm (survival rate), the
132 proportion of surviving females on the second patch (dispersal rate), and the proportion of surviving
133 females on the initial patch (remaining rate). We also recorded the state of dead females as either
134 drowning on the surrounding cotton or consumed by predators. Because *P. punctatus* always took the
135 prey mite away from the setup and because spider mites could not escape the setup (Otsuki and Yano
136 2014), we considered missing *T. kanzawai* females as having been consumed by *P. punctatus*. We
137 compared these rates between treatments using the generalized linear model with binomial error dis-
138 tribution (SAS Institute Inc. 2010) adjusted using Holm-Bonferroni correction.

139
140 Do generalist predatory mites prevent dispersal of spider mites?

141
142 To examine whether the generalist predatory mite *E. sojaensis* prevents dispersal of spider mites, we
143 created two-patch setups as shown in Fig. 2. Since webs build by one *T. kanzawai* female effectively

144 protect the female from *E. sojaensis* (Ozawa and Yano 2009; Yano 2012), and the leaf square used in
145 the above experiment (20×20 mm) was too large to be exhausted by a *T. kanzawai* female, we in-
146 troduced one mated *T. kanzawai* female onto each of 153 smaller bean leaf squares (10×10 mm;
147 initial patches). Since preliminary tests showed that *T. kanzawai* females in the absence of *E. sojaen-*
148 *sis* start dispersing from the setup on day 3, and that webs build for 3 days are effective against the
149 predators, we connected each leaf to another leaf square (10×10 mm; second patches) with a Para-
150 film bridge (10×30 mm; Fig. 2) after 3 days of the introduction. We then introduced one adult fe-
151 male *E. sojaensis* onto each of 80 setups (predator present), and 73 other setups served as controls
152 (predator absent). We did not introduce more than one predatory mite female on a setup because they
153 do not live in a group as a rule (Yano, unpublished). Because *E. sojaensis* females cannot penetrate
154 or walk on the complicated spider mite webs (Osakabe 1988), they prowled on the bridges and on the
155 second patches where spider mites could disperse.

156 After 24 h, we recorded the state of *T. kanzawai* females and calculated survival, dispersal,
157 and remaining rates as described above. Six setups in which *E. sojaensis* had escaped were excluded
158 from the data. Therefore, the numbers of replications were 74 (predator present) and 73 (predator
159 absent). The above rates were compared between treatment groups using Fisher's exact test (SAS
160 Institute Inc. 2010) with Holm-Bonferroni correction

161
162 Do specialist predatory mites promote patch colonization by spider mites?

163

164 To examine whether the specialist predatory mite *N. womersleyi* promotes dispersal of spider mites
165 and to demonstrate that the predator increases the number of prey patches, we introduced more than
166 one spider mite on a setup with more than two patches as shown in Fig. 3. We introduced five mated
167 *T. kanzawai* females onto each of 44 bean leaf squares (10×10 mm; initial patches) and allowed
168 them to oviposit for 24 h, which was sufficient to retain *N. womersleyi* on the patch (see Results). We
169 then introduced one adult female *N. womersleyi* onto each initial patch in 20 setups (predator pre-
170 sent), and the other 24 setups served as controls (predator absent). We did not introduce more than
171 one predatory mite on a setup because of the same reason described above. After allowing the preda-
172 tors 30 min of acclimation, we connected each initial patch in all setups to four leaf squares (10×10
173 mm; consecutive patches) linearly with Parafilm bridges (10×30 mm; Fig. 3).

174 After 2 days, when the differences between treatments were most conspicuous after predator
175 introduction, we recorded the number and state of *T. kanzawai* females on each patch and on the
176 bridge, and calculated survival and dispersal rates as described above. We also recorded the number
177 of newly colonized patches out of the four consecutive patches. We judged a patch with webs, injury
178 scars, eggs, and feces of *T. kanzawai* females as colonized regardless of the presence of females. Five
179 setups in which *N. womersleyi* had intruded into consecutive patches were excluded from the data.
180 Therefore, the numbers of replications were 15 (predator present) and 24 (predator absent), respec-
181 tively. The above rates were compared between treatment groups using the generalized linear model

182 with binomial error distribution (SAS Institute Inc. 2010) adjusted using Holm-Bonferroni correc-
183 tion.

184

185 **Results**

186

187 Do ants prevent dispersal of spider mites?

188

189 In the presence of ants, significantly fewer *T. kanzawai* females survived and dispersed to the second
190 patch than in the absence of ants (Fig. 4a, b). All of the dead *T. kanzawai* females in the presence of
191 ants were preyed upon. On the other hand, the number of *T. kanzawai* females that remained on the
192 initial patch with the protective webs did not differ significantly between the treatments (Fig. 4c),
193 indicating that *T. kanzawai* females did not hesitate to move out of the refuges and disperse. There-
194 fore, it is likely that the ants lethally hindered the dispersal of *T. kanzawai* by consuming dispersing
195 females.

196

197 Do generalist predatory mites prevent dispersal of spider mites?

198

199 In both treatments, nearly all *T. kanzawai* females survived, and the survival rate did not differ sig-
200 nificantly between the treatments (Fig. 5a). All dead females in the presence of *E. sojaensis* were

201 drowned, not preyed upon by *E. sojaensis*. In the presence of *E. sojaensis*, significantly fewer *T.*
202 *kanzawai* females dispersed to the second patch than in the absence of *E. sojaensis* (Fig. 5b).
203 The proportion of *T. kanzawai* females that remained on the initial patch did not differ significantly
204 between the treatments (Fig. 5c), suggesting that *T. kanzawai* females that had moved out of the ini-
205 tial patch could not access or colonize the second patch in the presence of *E. sojaensis*. Thus, *E.*
206 *sojaensis* non-lethally prevented the dispersal of *T. kanzawai*.

207
208 Do specialist predatory mites promote patch colonization by spider mites?

209
210 *Neoseiulus womersleyi* stayed under the webs on the initial patch. On the other hand, nearly all *T.*
211 *kanzawai* females survived under both treatments, and the survival rate did not differ significantly
212 between the treatments (Fig. 6a). None of the dead females was preyed upon by *N. womersleyi*. In
213 the presence of *N. womersleyi*, significantly more *T. kanzawai* females dispersed to other patches
214 (Fig. 6b), and females colonized significantly more patches in the presence than in the absence of *N.*
215 *womersleyi* (Fig. 6c). Therefore, *N. womersleyi* promoted the dispersal of *T. kanzawai*.

216 217 **Discussion**

218
219 By using a connected patch system that allowed prey dispersal toward an intact patch, we revealed

220 that generalist predators that cannot suppress spider mites in systems with no opportunity for disper-
221 sal effectively prevented spider mite dispersal between patches either by directly consuming dispers-
222 ing prey (density-mediated effects) or by making them hesitate to colonize intact patches
223 (trait-mediated effects).

224 Although the generalist predatory mites did not directly reduce the survival of *T. kanzawai*
225 females, the predators would reduce the chance of feeding and oviposition of *T. kanzawai* females
226 that could not either access or colonize intact patches. This may be one of the mechanisms by which
227 generalist predatory mites, which cannot penetrate protective webs produced by spider mites (espe-
228 cially most *Tetranychus* species) do suppress mites in the field (McMurtry 1985; Duso 1988, 1989;
229 James 1990; but see Croft and MacRae 1992). Unlike specialist predatory mites, which depend on
230 spider mites, generalist predatory mites subsist on plant-derived alternative foods such as pollen
231 (McMurtry and Johnson 1965; Kennett et al. 1979) and pearl bodies (Ozawa and Yano 2009), and
232 also on mildew infecting plants (Duso et al. 2003), which are relatively stable food resources com-
233 pared with spider mites. Therefore, ‘patrolling’ of host plants of spider mites by generalist predatory
234 mites is less correlated with spider mite density (McMurtry 1992).

235 *Tetranychus kanzawai* females did not hesitate to disperse in the presence of ants and were
236 preyed upon, whereas females did hesitate to colonize intact patches in the presence of generalist
237 predatory mites. The difference may be attributed to the ants’ higher ability to capture spider mites
238 due to their greater mobility and larger body size compared with predatory mites. Moreover, because

ants can approach and attack *T. kanzawai* females from the surrounding wet cotton barrier, which mites could not access, the females might not perceive approaching ants. In contrast, they may be vigilant to chemical cues of predatory mites (Grostal and Dicke 1999; Škaloudova et al. 2007; Bowler et al. 2013) that are confined on the leaves and bridges with the spider mites.

We also found that specialist predatory mites that suppress spider mites at high densities, let spider mites escape and colonize new patches in systems where spider mites could disperse toward intact patches. Previous studies also reported that specialist predatory mites promoted dispersal of the spider mites (Bernstein 1984; Grostal and Dicke 1999; Oku et al. 2004; Bowler et al. 2013). Although the experiment using setups with more than two patches apparently looks similar to the two-patch system used by Bowler et al. (2013), the two experiments qualitatively differ in that two-patch systems can only compare departure rates of mites from the initial patch, while systems with more than two patches can compare the number of newly colonized patches in the presence or otherwise of the predator. Thus, we further confirmed that the dispersal of spider mites in response to the attack of specialist predatory mites increased the number of colonized patches. Because *N. wormsleyi* females prefer spider mite eggs laid in the webs rather than adult females (Takafuji and Chant 1976; Fernando and Hassell 1980; Sabelis 1990; Blackwood et al. 2001; Furuichi et al. 2005), it is not surprising that all *T. kanzawai* females escaped predation while predatory mites stayed on the initial patch. We predict that specialist predatory mites can rarely follow dispersed spider mites in the wild, as there are many directions in which spider mites can escape. Although specialist predatory

258 mites in the genera *Phytoseiulus* and *Neoseiulus* can follow trails left by a group of spider mites, they
259 cannot follow a trail left by a single spider mite female (Yano and Osakabe 2009; Shinmen et al.
260 2010).

261 Dispersed spider mite females can establish local populations, which are often in danger of
262 extinction because of larger predatory insects (Janssen et al. 1998), coincidental intraguild predation
263 by larger herbivores (Shirotsuka and Yano 2012), and natural or human-induced disturbance (e.g.
264 Das 1959). Although specialist predatory mites would impose short-term fitness costs on spider mites
265 by consuming eggs (e.g. Takafuji and Chant 1976), the predatory mites may reduce the extinction
266 rate of spider mite metapopulations in the long term by increasing the number of local populations
267 (Levins 1969). On the other hand, generalist predators would impose long-term costs on spider mite
268 metapopulations by inhibiting establishment of local populations and by imposing short-term costs
269 on dispersing females as discussed above.

270 Contrary to conventional understanding, our results suggest that native generalist predators
271 can be more effective agents for conservation biological control against *Tetranychus* species than can
272 specialist predatory mites at least under some conditions. Particularly under low spider mite density,
273 specialist predatory mites would scatter spider mite females, increasing the number of infested
274 patches in the area. Moreover, specialist predators in general do not remain on a reward-less patch
275 (Charnov 1976; Symondson et al. 2002) Thus, specialist predatory mites can suppress spider mite
276 populations only under high spider mite density (e.g. Burnett 1979; Janssen et al. 1997; Schausberger

277 and Walzer 2001). From the viewpoint of conservation biological control strategy, using native gen-
278 eralist predatory mites that subsist on alternative food resources rather than specialist predatory mites
279 that depend on spider mites might maintain spider mites at low endemic densities. More importantly,
280 we suggest the significant lethal impacts of ants on spider mites that have not been considered in
281 discussions of conservation biological control against spider mites (but see Osborne et al. 1995). The
282 relative effects of generalist and specialist predators, as well as interactions between them, should be
283 examined in future studies in terms of sustainable management of spider mites.

284

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286

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451

Figure captions

453

454 **Fig. 1** Experimental setup for testing whether the generalist ant *Pristomyrmex punctatus* prevent
455 dispersal of *Tetranychus kanzawai*. The two-patch setup was placed in a microcosm with and without
456 ants

457

458 **Fig. 2** Experimental setup to compare the dispersal of *Tetranychus kanzawai* in the presence or ab-
459 sence of the generalist predatory mite *Euseius sojaensis* that cannot penetrate spider mite webs

460

461 **Fig. 3** Experimental setup to compare the dispersal and new patch foundation of *Tetranychus*
462 *kanzawai* in the presence or absence of the specialist predatory mite *Neoseiulus womersleyi* that pen-
463 etrates spider mite webs

464

465 **Fig. 4** Effects of the generalist ant *Pristomyrmex punctatus* on (a) survival, (b) dispersal and (c) re-
466 maining rates (mean +SE) of the spider mite *Tetranychus kanzawai*. Asterisks indicate a significant
467 difference at $P < 0.01$ by the generalized linear model with binomial error distribution adjusted using
468 Holm-Bonferroni correction.

469

470 **Fig. 5** Effects of the generalist predatory mite *Euseius sojaensis* on (a) survival, (b) dispersal and (c)

471 remaining rate of the spider mite *Tetranychus kanzawai*. An asterisk indicates a significant differ-
472 ence at $P < 0.01$ by Fisher's exact test with Holm-Bonferroni correction.

473

474 **Fig. 6** Effects of the specialist predatory mite *Neoseiulus womersleyi* on (a) survival, (b) dispersal
475 and (c) patch colonization (mean + SE) of the spider mite *Tetranychus kanzawai*. Asterisks indicate a
476 significant difference at $P < 0.05$ by the generalized linear model with binomial error distribution ad-
477 justed using Holm-Bonferroni correction.

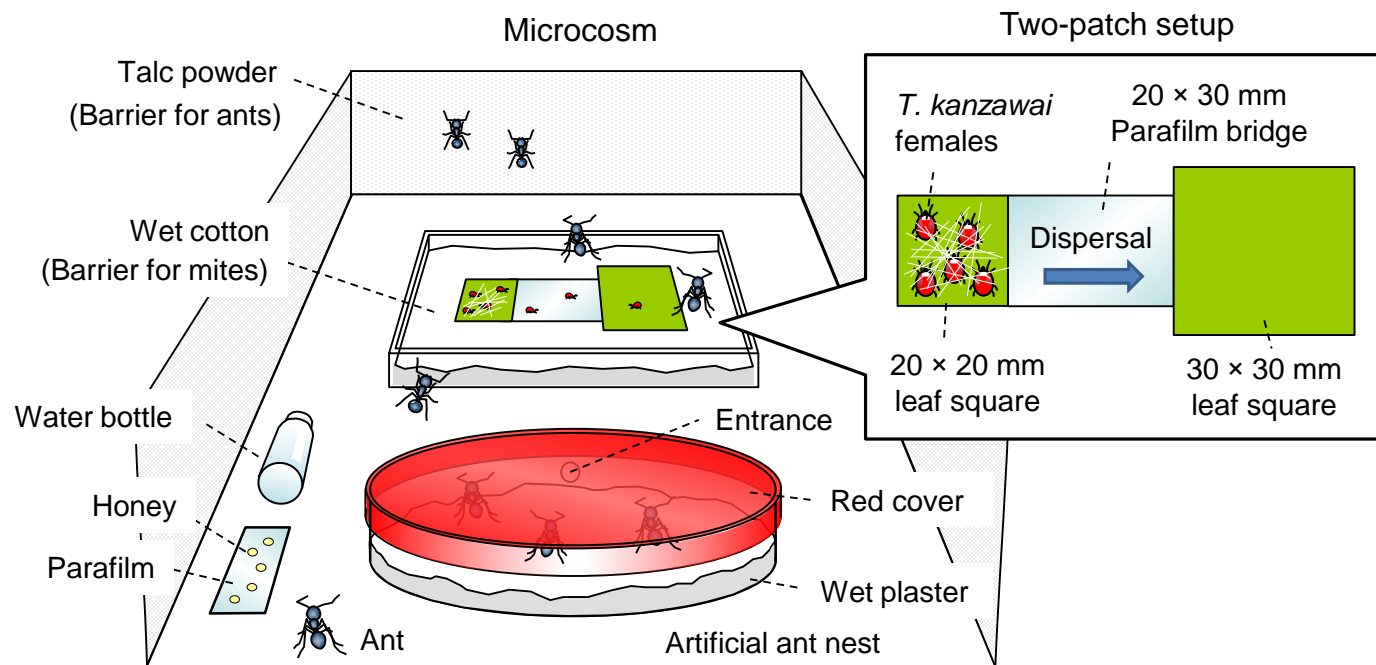


Fig 1

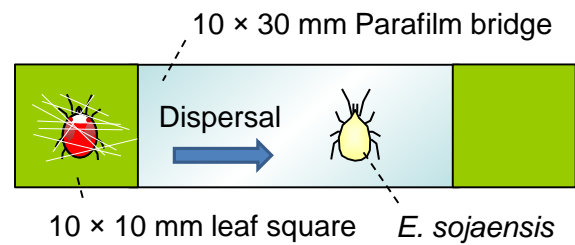


Fig 2

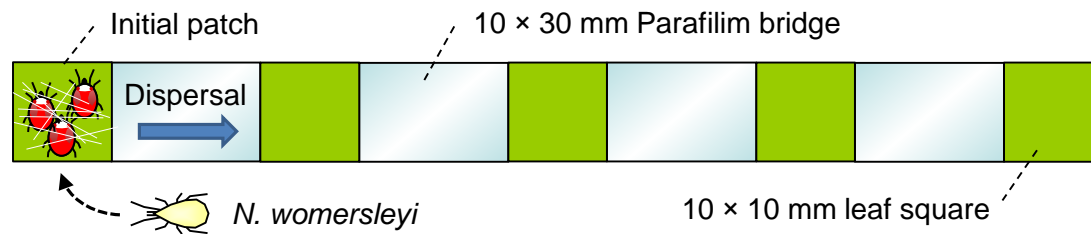


Fig 3

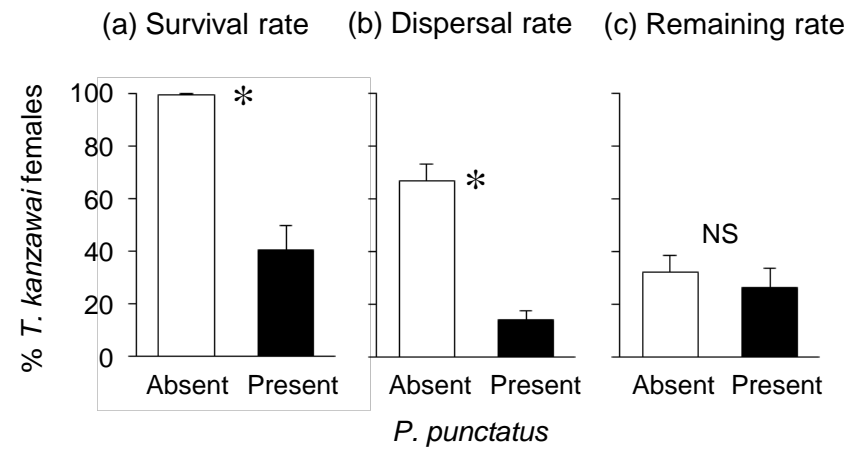


Fig 4

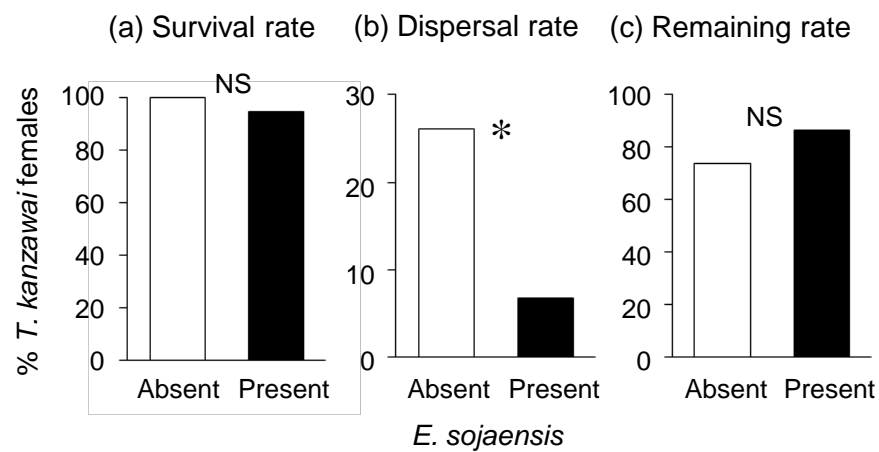


Fig 5

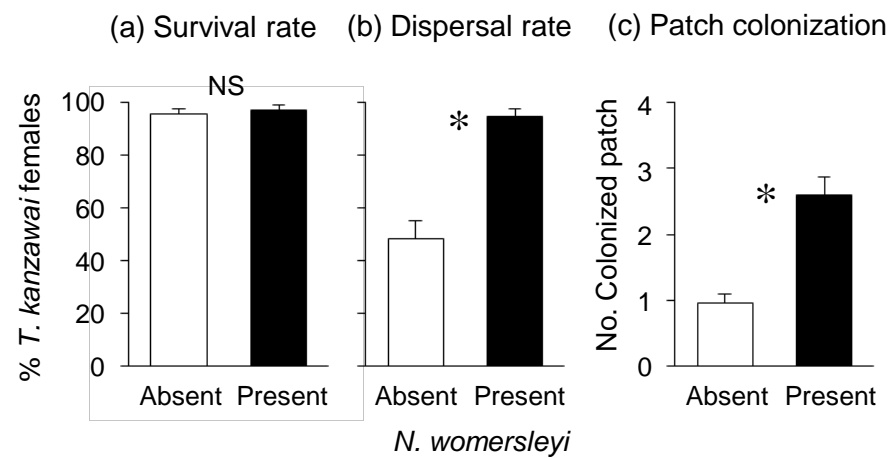


Fig 6